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Apomixis in Neotropical Vegetation

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Abstract

In neotropical ecosystems, genetic variability and diversity of plant species seem to be generated and maintained by sexual reproduction. However, apomixis appears as an alternative reproductive strategy in many plant families. Apomixis comprises the development of a new organism from an unreduced and unfertilized egg cell. Traditionally, it is considered a dead end of evolution due to the lack of genetic variability; however, processes such as *de novo* mutation, gene conversion, mitotic recombination and epigenetic drift may work as important sources of genetic variation during apomictic reproduction. Moreover, plant species show facultative apomixis, which allows the formation of sexual and asexual offspring. As a result, natural apomict populations show greater genotypic variability than expected from a clonal population. Also, asexual reproduction is considered one of the important attributes promoting diversity in angiosperms. Here, I review the occurrence of apomixis in several plant families that are well represented in neotropics and I infer the relation between apomixis and diversity of species. Many plant families that are common in the neotropical region show facultative apomixis associated with polyploidy and hybridization events. Apomixis seems to play a key role in the establishment of new evolutionary lineages in a wide variety of environmental conditions.

Keywords: asexual reproduction, diversity, genetic variability, plant diversity, tropical vegetation

1. Introduction

The tropics, subdivided into paleotropics and neotropics, include the region of the earth's surface between Tropic of Cancer (23°27'N) and the Tropic of Capricorn (23°27'S) and comprise about 40% of the earth's land surface [1]. As currently defined by Schultz [2], the neotropical ecozone extends from central Mexico in the north to southern Brazil in the south, including Central America, the Caribbean islands and most of South America. Comprising around 90,000–110,000 species of seed plants, the neotropics harbors about 37% of the world's species

[3]. This great diversity is allocated in different vegetation formations such as wet and dry forests, desert areas and savanna formations, which show very variable environmental conditions. A recent survey about world biodiversity has revealed that some countries of the neotropical region are among the world's 10 most megadiverse [4]. Brazil, the most megadiverse country in the world considering plants and fungi, presents its biodiversity distributed in six major phytogeographical domains. In addition, each phytogeographical domain presents a wide variety of vegetation types, habitats and microhabitats that are occupied by a wide diversity of plants, fungi and animals [4].

Many mechanisms have been proposed to have played a role in the historical assembly and evolution of neotropical biodiversity [3]. Among these mechanisms, the plant-animal interactions seem to play a relevant role in the generation of genetic diversity of plant species, through gene flow conducted via pollination and seed dispersal [3]. In addition, genetic variability seems to be generated and maintained also by the predominance of genetically controlled self-incompatibility systems. Self-incompatibility (SI) has been found to be the main breeding system in forest [5, 6], savanna [7] and semi-arid [8] communities. However, most of these studies evaluated the breeding systems of tree species. In herbaceous community and for species in disturbed areas usually with an inefficient pollination fauna, the lowest frequencies of self-incompatibility have been reported [9].

Despite the predominance of sexual reproduction, a growing number of studies on breeding systems have demonstrated the presence of apomixis as an alternative reproductive strategy of the plants of neotropical biomes [10]. Apomixis, the asexual reproduction via seed, comprises the development of a new organism from an unreduced and unfertilized egg cell [11]. It prevents meiosis and fertilization leading to a clonal progeny and presents a sexual development that is deregulated at several stages where meiosis is impaired or absent resulting in an unreduced female gametophyte, fertilization is avoided leading to the production of an autonomous embryo and the endosperm development is autonomous or sexual [12, 13]. Thus, three elements are commonly observed in apomicts: (1) the generation of a cell capable of forming an embryo without prior meiosis (apomeiosis); (2) the spontaneous, fertilization-independent development of the embryo (parthenogenesis); (3) and the capacity to either produce endosperm autonomously or to use a pseudogamous endosperm derived from fertilization [11, 13].

Studies suggest that apomixis may emerge from the sexual system deregulated by genetic and epigenetic modifications, which entails in the alteration or omission of stages of the sexual development [14–16]. The genomic changes can often be a response to the consequences of genome shock that occurs in allopolyploids [17]. The most accepted hypothesis for the association between allopolyploidy and apomixis, at least for gametophytic apomixis, is that apomixis can be caused by the asynchronous expression of duplicate genes [13, 14], which leads to important changes in the stages of the sexual program as early initiation of the embryonic sac and embryogenesis from atypical sites and times during the reproduction. According to the 'hybridization theory' postulated by Carman [14], the hybridization of two sexual ecotypes or related species with different reproductive characters contributes to the induction of apomictic phenomena. On a mechanistic level, this results from hybrid plants containing two sets of parental genes that are involved in female embryo sac development; the asynchronous expression of these duplicated genes leads to precocious embryo sac initiation and embryogenesis

at aberrant sites during reproduction [18]. In this sense, the combination of hybridization and polyploidy would be responsible for changes in important processes during stages of megasporogenesis, megagametogenesis and fertilization, leading to apomixis [19].

Even though the frequent association between polyploidy/allopolyploidy and gametophytic apomixis is seen, several studies with tropical plants have demonstrated the occurrence of sporophytic apomixis (adventitious embryony) in polyploid taxa, which generally form polyploid complexes with a wide geographic distribution [20–22].

Several advantages are attributed to apomicts such as: (1) to allow reproduction even in the absence of pollinators; (2) to promote clonal reproduction through seeds, that is, to produce individuals genetically equal to the parental plant, but maintaining the advantages associated with the seeds as protection, dispersion and dormancy of the embryo; (3) to avoid costs associated with meiosis in cases where it is absent; (4) to avoid the costs associated with pollen grains' production in plants with low percentages of viable pollen grains or total male sterility; (5) to allow the establishment of extremely adapted genotypes to a specific environment, especially in apomictic species originated from polyploid hybrids, considered highly heterozygous and very vigorous [19]. For agriculture, apomixis is an attractive trait for the enhancement of crop species because it mediates the formation of large genetically uniform populations and perpetuates hybrid vigor through successive seed generations. Thus, apomixis is of practical interest to breeders as a means of fixation of highly complex genotypes including hybrid cultivars [13, 23]. Also, apomixis can be a viable alternative to increase the food production and, at the same time, reduce the deforestation of native vegetation [13].

2. Types of apomixis

Several types of apomixis have been identified in plants. In general, types of apomixis can be classified according to the origin and location of the somatic cell that gives rise to the embryo, the need or not of fecundation for the formation of endosperm and the possibility or not of occurrence along with sexual reproduction [18, 19]. The embryo can form within an embryo sac produced entirely from mitotic events in the gametophytic apomixis or directly from somatic cells surrounding the developing sexual embryo sac in the sporophytic apomixis. In some cases, fertilization is required for endosperm development and subsequent seed viability (pseudogamy), but in others, the endosperm can develop autonomously. Furthermore, most apomictic plants are facultative, meaning that sexual and asexual reproduction can occur concurrently [18].

In the gametophytic apomixis, changes in specific stages of the sexual process lead to the absence of reductive meiosis in the formation of the embryo sac (mitotic formation of unreduced embryo sacs), to the autonomous development of the embryo and adaptation in the formation of the endosperm. The embryo is formed parthenogenetically of the egg cell, located inside an unreduced embryo sac. This type of apomixis is subdivided into two forms, diplospory and apospory, depending on the origin of the cell that initiates unreduced embryo sac formation. In the diplospory, the unreduced embryo sac originates from the megaspore mother cell by suppression or modification of meiosis. In the apospory, the unreduced embryo sac originates from a somatic cell of the ovule, usually of the nucellus. Unlike diplospory in

which there is commitment of the sexual reproduction, in the apospory, several nucellar cells can differentiate and give rise to multiple somatic embryonic sacs in a single ovule, while the megaspore mother cell originates a reduced embryo sac leading to the coexistence of the apomictic and sexual processes in the same ovule [12, 19].

In the sporophytic apomixis, also called adventitious embryony, the embryo originates directly from cells of the nucellus or the integument of the ovule. Commonly, adventitious embryony occurs associated with sexual reproduction and the apomictic embryo survival depends on successful fertilization of the meiotically derived embryo sac and its ability to grow sufficiently to gain access to the nutrient endosperm [12].

While adventitious embryony appears to be more common in tropical trees and shrubs, gametophytic apomixis is described primarily in herbaceous and perennial plants of temperate regions [24]. Gametophytic apomixis occurs most commonly among three families of angiosperms, Asteraceae, Rosaceae and Poaceae, but has been reported from at least 17 other families as well. For the plant families that occur in neotropical region, in addition to Asteraceae, Poaceae and Rosaceae, apospory was reported in Adoxaceae, Amaranthaceae, Araceae, Boraginaceae, Brassicaceae, Cucurbitaceae, Dioscoreaceae, Erythroxylaceae, Euphorbiaceae, Fabaceae, Hypericaceae, Lauraceae (*Lindera*), Magnoliaceae, Melastomataceae, Ochnaceae, Orchidaceae, Plantaginaceae, Polygonaceae, Ranunculaceae, Rutaceae and Urticaceae. Diplospory, also predominant in Asteraceae, Poaceae and Rosaceae, was recorded in other 16 families: Amaranthaceae, Amaryllidaceae, Balanophoraceae, Brassicaceae, Burmanniaceae, Cactaceae, Cucurbitaceae, Ochnaceae, Orchidaceae, Orobanchaceae, Plumbaginaceae, Potamogetonaceae, Rhamnaceae, Saururaceae, Thymelaeaceae and Urticaceae. Adventitious embryony, common in tropical vegetation, was registered in 48 plant families that occur in neotropics: Adoxaceae, Amaranthaceae, Amaryllidaceae, Anacardiaceae, Apiaceae, Apocynaceae, Araceae, Asparagaceae, Asteraceae, Bignoniaceae, Boraginaceae, Brassicaceae, Burseraceae, Cactaceae, Capparaceae, Caricaceae, Celastraceae, Clusiaceae, Combretaceae, Cucurbitaceae, Euphorbiaceae, Fabaceae, Lecythidaceae, Malpighiaceae, Malvaceae, Melastomataceae, Meliaceae, Moraceae, Myrtaceae, Ochnaceae, Onagraceae, Orchidaceae, Phyllanthaceae, Poaceae, Polygonaceae, Ranunculaceae, Rhamnaceae, Rosaceae, Rubiaceae, Rutaceae, Salicaceae, Sapindaceae, Smilacaceae, Solanaceae, Symplocaceae, Thymelaeaceae, Urticaceae and Zygophyllaceae. As previously mentioned, adventitious embryony was the most common type of apomixis in neotropical plants. In addition, this type of apomixis predominated in plant families with high diversity in this region. Examples are families well represented in the Brazilian vegetation such as: Apocynaceae (850 species in Brazil), Bignoniaceae (350 species), Euphorbiaceae (ca. 1000 species), Fabaceae (1500 species), Malvaceae (400 species), Myrtaceae (ca. 1000 species) and Orchidaceae (ca. 2500 species) [25]. Detailed information is in the next topic (apomixis in the neotropical region).

3. Apomixis in the neotropical region

Apomixis is relatively prevalent among angiosperms, with a pattern of distribution that suggests that it has evolved many times [13, 26]. It has been described in 32 orders, 78 families and 293 species [14, 26], and it is well represented among both monocotyledonous, eudicotyledonous

and basal angiosperms [13]. Several authors have noted a marked bias in the distribution of apomixis among angiosperms. Of the plants known to use gametophytic apomixis, 75% of confirmed examples belong to three families, the Asteraceae, Rosaceae and Poaceae. Some authors have postulated that the current patterns of distribution may reflect the predisposition of certain plant groups to the unique developmental and genetic changes that characterize apomixis. But some of this bias also might relate to the ease of embryological examination in some plant groups or to data accumulated from embryological investigations associated with activities in crop improvement.

There are other noted associations between apomixis and various plant life history traits that provide insights into the nature and possible ecological role of this phenomenon. Apomixis frequently is associated with the expression of mechanisms that limit self-fertilization. Many apomictic plants belong to genera in which sexual members predominantly exhibit physiological self-incompatibility, dioecy or heterostyly [27]. An example in the neotropical region is Bignoniaceae. In this family, diploid taxa are generally self-incompatible, mainly exhibiting late-acting self-incompatibility [28]. However, polyploid species and populations often are self-compatible and exhibit asexual reproduction [22, 29].

Following are examples of orders and families well represented in the neotropical region that have apomictic taxa. Information on the occurrence of apomixis in families were extracted from Salomão and Allem [10], Carman [14], Batygina et al. ([30], Orchidaceae), Apomixis Database [31] and the open access articles. The occurrence of families in the neotropical region was confirmed in Flora do Brasil website [25], Angiosperm Phylogeny Group website [32], and Tropicos website [33].

3.1. Alismatales

Apomixis was reported in Araceae (*Aglaonema* and *Spathiphyllum*) and Potamogetonaceae (*Potamogeton*). In Araceae, adventitious embryony was determined for *Spathiphyllum patinii*, a Colombian species. In Potamogetonaceae, diplospory was observed in *Potamogeton obtusifolius*, species that does not occur in the tropical region.

3.2. Asparagales

Apomixis was reported in Amaryllidaceae, Asparagaceae, Hemerocallidaceae and Orchidaceae. In all families, gametophytic and sporophytic apomixis were recorded, but adventitious embryony predominate. In Orchidaceae, the most representative plant family in the neotropics among these cited families, polyembryony is frequent. The presence of several embryos in a single seed has been mentioned in certain tropical species, but this feature rarely occurs in species growing in temperate zone. Apomixis is present in 16 genera (*Cephalanthera*, *Corunastylis*, *Cynorchis*, *Cynosorchis*, *Dactylorhiza*, *Epidendrum*, *Epipactis*, *Gastrodia*, *Gymnadenia*, *Maxillaria*, *Neottia*, *Nigritella*, *Orchis*, *Spiranthes*, *Zeuxine* and *Zygopetalum*) [30]. Most genera of Orchidaceae species showed adventitious embryony, but *Corunastylis*, *Cynosorchis* and *Zygopetalum* showed both gametophytic and sporophytic apomixis. Only *Dactylorhiza* has aposporous taxa.

3.3. Asterales

In Asterales, apomixis was reported only in Asteraceae, the most diverse family of this order. In this plant family, gametophytic apomixis occurs in 27 genera and, adventitious embryony and diplospory were recorded in *Hieracium*. Apospory was recorded in *Calotis*, *Campovassouria*, *Campuloclinium*, *Cineraria* (Senecio), *Crepis*, *Eurybiopsis*, *Gutierrezia*, *Minuria* and *Pilosella*. Diplospory occurs in *Ageratina*, *Arnica*, *Blumea*, *Brachycome*, *Chondrilla*, *Chromolaena*, *Gyptis*, *Ixeris*, *Leontopodium*, *Praxelis*, *Rudbeckia*, *Taraxacum* and *Townsendia*. In genera such as *Antennaria*, *Erigeron*, *Eupatorium* and *Parthenium*, apospory and diplospory are observed. The phylogenetic distribution indicates that apomixis occurs mainly in the subfamily Asteroideae [34], restricting to polyploid cytotypes. Among tropical genera, the diplospory predominate.

3.4. Boraginales (?)

Apomixis was reported in three genera of Boraginaceae: *Cordia*, *Cynoglossum* and *Trichodesma*. Apospory is present in *Cordia* and *Cynoglossum*, while adventitious embryony is present in *Trichodesma*.

3.5. Brassicales

Gametophytic and sporophytic apomixis were reported in two genera of Brassicaceae: *Boechera* (apospory, diplospory and adventitious embryony) and *Iberis* (apospory and diplospory). Adventitious embryony was reported in Capparaceae (*Capparis*), Caricaceae (*Carica*) and Trapeolaceae (*Trapeolum*).

3.6. Caryophyllales

Apomixis was reported in four families: Amaranthaceae, Cactaceae, Polygonaceae and Plumbaginaceae. In Amaranthaceae, diplospory was observed in the genus *Aerva*, while both gametophytic and sporophytic apomixis were observed in *Beta*. In Cactaceae is described the occurrence of adventitious embryony in *Haageocereus* (*H. tenuis*; [35]); and *Mammillaria*, *Opuntia* and *Pereskia*; in *Opuntia* was also reported the occurrence of diplospory. In Polygonaceae, apospory and adventitious embryony were reported in *Atraphaxis*, and in Plumbaginaceae, diplospory was observed in *Limonium* (*Statice*).

3.7. Celastrales

In Celastraceae is described the occurrence of adventitious embryony in *Celastrus* and *Euonymus*.

3.8. Cucurbitales

Apomixis was reported in five genera of Cucurbitaceae: *Cucumis* (apospory, diplospory and adventitious embryony), *Luffa* (diplospory), *Marah* (apospory), *Momordica* (diplospory and adventitious embryony) and *Sicyos* (adventitious embryony).

3.9. Dioscoreales

In this order, gametophytic apomixis was reported in two plant families: Burmanniaceae (*Burmannia* com diplospory) and Dioscoreaceae (*Tacca* with apospory).

3.10. Dipsacales

Apomixis was reported in Adoxaceae and Caprifoliaceae. In Adoxaceae, apospory and adventitious embryony were described in *Sambucus*, and in Caprifoliaceae, adventitious embryony was observed in the genus *Scabiosa*.

3.11. Ericales

In this order, apomixis was described in four families: Cyrillaceae, Lecythidaceae, Primulaceae and Symplocaceae. In Cyrillaceae, apospory was reported in *Cliftonia*. In the other families, adventitious embryony was registered in *Cariniana* (Lecythidaceae) (*C. estrellensis*, typical species of the neotropical savanna), *Ardisia* (Primulaceae) and *Symplocus* (Symplocaceae).

3.12. Fabales

Apomixis was reported only in Fabaceae, where there was a predominance of adventitious embryony. *Trifolium* was the only genus registered with apospory. *Acacia*, *Cassia*, *Copaifera* and *Millettia* showed adventitious embryony. *Acacia polyphila* and *Copaifera langsdorffii* are well-represented polyembryonic species of neotropical savannas [10].

3.13. Gentianales

In Gentianales, adventitious embryony was registered in Apocynaceae and Rubiaceae. In Apocynaceae is described the occurrence of adventitious embryony in *Cynanchum*, *Hancornia* and *Vincetoxycum*. *Hancornia speciosa* is a typical polyembryonic species of neotropical savannas [10]. In Rubiaceae, adventitious embryony was confirmed for *Genipa americana*; the type of apomixis was not determined in the genus *Coprosma*.

3.14. Lamiales

Apomixis was registered in three families: Bignoniaceae, Orobanchaceae and Plantaginaceae. In Bignoniaceae is described the occurrence of adventitious embryony in polyploid and polyembryonic species of *Anemopaegma* [21, 36, 37] and *Handroanthus* [22, 38] (**Figure 1**). In Orobanchaceae, diplospory was reported in *Cistanche* and *Orobanche*, and in Plantaginaceae, apospory was observed in *Globularia*.

3.15. Laurales

In this order, apospory was registered in Lauraceae in the genus *Lindera*.

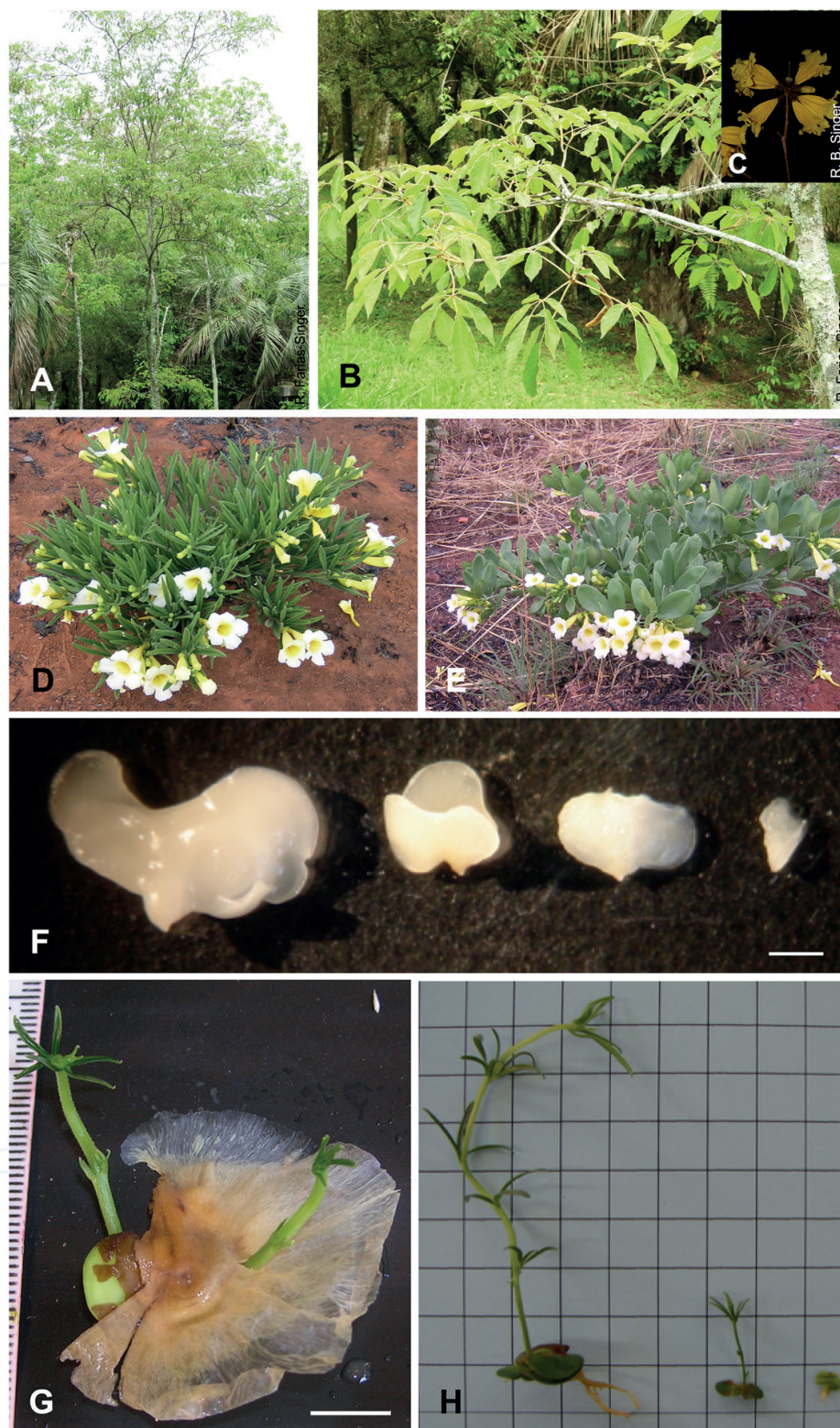


Figure 1. Apomictic species of Bignoniaceae. (A–C) *Handroanthus chrysotrichus* (Mart. ex A. DC.) Mattos: (A) tree; (B) branches; (C) flowers. (D) *Anemopaegma arvense* (Vell.) Stellf. ex de Souza. (E) *Anemopaegma glaucum* Mart. ex DC. (F) Embryos of polyembryonic seeds of *Anemopaegma* species. (G and H) Polyembryonic seedlings of *Anemopaegma* species. Photos (A) and (B) provided by Rosana Farias-Singer; photo (C) provided by Rodrigo Bustus Singer; photos (D–H) provided by Fabiana Firetti.

3.16. Liliales

Apomixis was reported in Liliaceae, Melanthiaceae and Smilacaceae with the predominance of adventitious embryony. In Liliaceae, *Erythronium* and *Tulipa* (*Amana*) showed adventitious embryony, while in *Lilium* diplospory was observed. In Melanthiaceae, adventitious embryony was recorded in *Trillium*, and in Smilacaceae, it was recorded in *Smilacina*.

3.17. Magnoliales

Apomixis was reported in Annonaceae and Magnoliaceae. In Annonaceae, apomixis was suggested for the production of fruits in *Cymbopetalum brasiliense*, species from Atlantic forest; however, the type of apomixis was not determined [39]. In Magnoliaceae, apospory was recorded in *Woonyoungia*.

3.18. Malpighiales

Apomixis was recorded in eight plant families: Clusiaceae, Erythroxylaceae, Euphorbiaceae, Hypericaceae, Malpighiaceae, Ochnaceae, Phyllanthaceae and Salicaceae. Clusiaceae was characterized by adventitious embryony, which was recorded in *Clusia* and *Garcinia* [40]. In Erythroxylaceae, apospory was recorded in *Erythroxylum*. In Euphorbiaceae, adventitious embryony was recorded in *Alchornea* (*Coelebogyne*), *Cnidoscolus* (*Jussieuia*), *Euphorbia* and *Mallotus*, while apospory was observed in *Manihot*. In Hypericaceae, apospory was recorded in *Hypericum*. Malpighiaceae was characterized by adventitious embryony that occurred in all genera in which apomixis was recorded such as *Aspicarpa*, *Banisteriopsis*, *Byrsonima* (in *B. basiloba*, typical species of the Cerrado [10]), *Galphimia* (*Thryallis*), *Heteropterys*, *Hiptage*, *Malpighia* and *Stigmaphyllon*. However, occurrence of apospory was also observed in *Hiptage*. In Ochnaceae, gametophytic and sporophytic apomixis were recorded in *Ochna*. In Phyllanthaceae, adventitious embryony was recorded in *Uapaca*, and in Salicaceae, this type of apomixis was observed in *Salix*.

3.19. Malvales

In this order, apomixis was reported in Malvaceae, Melastomataceae and Thymelaeaceae. In Malvaceae, particularly in the subfamily Bombacoideae, the occurrence of adventitious embryony was reported in *Bombacopsis* (*B. glabra*), *Pachira* (*P. oleaginea*) and *Eriotheca* (*E. gracilipes* and *E. pubescens* [20, 41]). The formation of polyembryonic seeds is reported in apomictic species of the group, as well as the occurrence of polyploidy. In Melastomataceae, most of the apomictic species occurs in Brazil. Apomictic species are described as autonomous, and in many of these, the total or partial unviability of the pollen grains is common [19, 51]. In this group, adventitious embryony was described in *Leandra* (*L. australis*), *Melastoma* (*M. malabathricum*), *Osbeckia* (*O. hispidissima*) and *Sonerila* (*Sonerila wallichii*); diplospory was recorded in *Leandra* (*L. australis*) and *Miconia* (*M. albicans*); and apospory was observed in *Clidemia* (*C. hirta*) and *Miconia* (*M. fallax*) [19]. In Thymelaeaceae, adventitious embryony was reported in *Daphne* and diplospory was registered in *Wikstroemia*.

3.20. Myrtales

This order was characterized by adventitious embryony that was recorded in Combretaceae, Myrtaceae and Onagraceae. In Combretaceae, apomixis was observed in *Combretum* (*Poivrea*). In Myrtaceae, adventitious embryony was recorded in *Callistemon*, *Eugenia* and *Syzygium*. In Onagraceae, adventitious embryony was reported in *Clarkia*, *Epilobium* (*Zauschneria*) and *Oenothera*.

3.21. Piperales

In this order, diplospory was recorded in Saururaceae in the genus *Houttuynia*.

3.22. Poales

Apomixis was recorded only in Poaceae that is characterized by apospory [14]. Apospory occurs exclusively in 41 genera (*Antheophora*, *Anthoxanthum*, *Apluda*, *Arundinella*, *Bouteloua*, *Brachiaria*, *Buchloe*, *Capillipedium*, *Chionachne*, *Chloris*, *Cortaderia*, *Dactylis*, *Danthonia*, *Echinochloa*, *Eragrostiella*, *Eremopogon*, *Eriochloa*, *Eustachys*, *Fingerhuthia*, *Harpochloa*, *Heteropogon*, *Hilaria*, *Hyparrhenia*, *Ischaemum*, *Lamprothyrsus*, *Merxmuellera*, *Panicum*, *Pentaschistis*, *Rendlia*, *Rhynchelytrum*, *Schima*, *Schizachyrium*, *Schmidtia*, *Setaria*, *Themeda*, *Thrasya*, *Thyrsostachys*, *Trachys*, *Tribolium*, *Tricholaena* and *Urochloa*). The occurrence of apospory with diplospory was recorded in *Dichanthium*, *Nardus* and *Paspalum*. Apospory and adventitious embryony were recorded in *Bothriochloa* and *Eulaliopsis*. Diplospory occurs exclusively in seven genera (*Calamagrostis*, *Elymus* (*Agropyron*), *Eragrostis*, *Phleum*, *Potamophila*, *Saccharum* and *Tripsacum*), and adventitious embryony occurs exclusively in *Bromus*, *Cenchrus* and *Oryza*. Apospory, diplospory and adventitious embryony were recorded in *Pennisetum*, *Poa* and *Sorghum*. In this family, apomixis is also related to polyploidy and is particularly common in tetraploids.

3.23. Ranunculales

Apomixis was registered in Ranunculaceae. Apospory was observed in *Ranunculus* and adventitious embryony was recorded in *Thalictrum*.

3.24. Rosales

In Rosales, apomixis was recorded in five families: Cannabaceae, Moraceae, Rhamnaceae, Rosaceae and Urticaceae. In Cannabaceae, apomixis was cited in *Humulus*, but the type of apomixis was not determined. In Moraceae, adventitious embryony predominate and was registered in *Ficus*, *Morus* and *Streblus*. In Rhamnaceae, diplospory was observed in *Pomaderris* and adventitious embryony was reported in *Zizyphus* (*Z. joazeiro*, species occurring in *Caatinga*, biome exclusive of Brazil). Rosaceae is characterized by gametophytic apomixis, which occurs exclusively in 10 genera (apospory in *Agrimonia*, *Amelanchier*, *Aphanes*, *Cotoneaster*, *Photinia* and *Sanguisorba*; apospory plus diplospory occur in *Crataegus*, *Rubus* and *Sorbopyrus*; diplospory occurs in *Parageum*). Despite the predominance of gametophytic apomixis in this family, adventitious embryony also occurs in several genera along with one or both types

of gametophytic apomixis (adventitious embryony plus apospory in *Alchemilla*, *Chaenomeles*, *Malus* and *Pyrus*; adventitious embryony, apospory and diplospory in *Potentilla* and *Sorbus*). In Urticaceae, diplospory occurs in *Boehmeria* and *Dorstenia* and gametophytic and sporophytic apomixis were registered in *Elatostema*.

3.25. Santalales

In this order, diplospory was described in Balanophoraceae, genus *Balanophora*.

3.26. Sapindales

In Sapindales, apomixis was reported in five families: Anacardiaceae, Burseraceae, Meliaceae, Rutaceae and Sapindaceae. In all families, adventitious embryony predominate, except in *Skimmia* (Rutaceae) where apospory occurs. In Anacardiaceae, adventitious embryony was registered in species with polyembryonic seeds of *Astronium*, *Mangifera*, *Myracrodruon* and *Tapirira*; *Astronium fraxinifolium*, *Myracrodruon urundeuva* and *Tapirira guianensis* are typical species of neotropical savannas of Brazil. In Burseraceae, adventitious embryony was registered in *Commiphora* (*C. leptophloeos*, typical species of neotropical savannas of Brazil) and in *Garuga*. In Meliaceae, adventitious embryony occurs in *Aphanamixis* and *Lansium*. In Rutaceae, adventitious embryony also occurs in polyembryonic species of 10 genera (*Aegle*, *Citrus*, *Feroniella*, *Fortunella*, *Murraya*, *Poncirus*, *Ptelea*, *Ruta* (*Haplophyllum*), *Triphasia* and *Zanthoxylum* (*Xanthoxylum*). Among the native representatives of Brazil, apomixis is described in *Galipea jasminiflora*. In Sapindaceae, adventitious embryony was described in polyembryonic species of *Magonia* (*M. pubescens*), which is also typical of neotropical savannas of Brazil.

3.27. Solanales

In this order, adventitious embryony was registered in five genera of Solanaceae: *Lycopersicon* (*Solanum*), *Petunia*, *Scopolia*, *Solanum* and *Withania*.

3.28. Zygophyllales

In this order, adventitious embryony was recorded only in Zygophyllaceae, genus *Zygophyllum*.

4. Apomixis and geographical distribution

In a number of plant and animal groups, it has been shown that sexual and asexual taxa exhibit different ranges of distribution, a phenomenon referred to as “geographical parthenogenesis” [42, 43]. Some studies conclude that parthenogenetic lineages tend to be found at higher latitudes, at higher elevations, in more xeric conditions, in more disturbed areas and on more island-like habitats than their sexual relatives. Bierzychudek [44] and Hörandl [45, 46] provided a comprehensive evaluation on the topic and concluded that apomictic plant groups have: (1) larger distributions, often considerably exceeding those

of their sexual relatives; (2) tend to range higher latitudes and altitudes than their sexual relatives and (3) tend to colonize previously glaciated areas. It is also true that sexual relatives often have distributions centered within much larger ranges of apomictic complexes. Accordingly, geographical parthenogenesis seems to be applied only to taxa with gametophytic apomixis. Sporophytic apomixis, which is frequently observed in multiseeded tropical plants, has completely different developmental and control mechanisms and is connected with other ecological and geographical features [46]. However, Hojsgaard and Hörandl [47] demonstrated that sporophytic and gametophytic apomixis exhibit similar patterns of distribution across climate zones.

Taxa with uniparental reproduction, such as apomixis and self-fertilization, intrinsically possess the potential to colonize new environments by single individuals [46], because both breeding systems can provide reproductive assurance independently from pollinators or mating partners. In the case of apomixis, apomictic individuals do not require any pollinators or mating partners because they generate their seeds either independently of pollen (autonomous) or are able to use self-pollen for fertilization and formation of the endosperm (pseudogamy) [48]. Different hypothesis has been raised to explain the ability of colonization of marginal habitats by apomictic taxa [49]. However, these hypotheses focus on the fact that the great majority of apomictic taxa emerged from hybridization and polyploidization events, which confer to these taxa genomic features, which could provide more physiological and ecological flexibility to adapt to severe conditions. Such events are considered the main promoters of genomic evolution. The whole-genome doubling can be accompanied by gene silencing, diversification in gene expression, differential gene expression of gene copies, and epigenetic changes, important alterations for the generation of phenotypic plasticity and rapid adaptation [49]. In addition, the association among hybrid origin, polyploidization and sexuality in facultative apomixis establish multiple discrete arrays of “clones” featuring different and diverse genotypes (Vrijenhoek’s frozen niche variation model). In this case, natural selection can cause partitioning among the “clonal” lineages and, thus, some apomictic genotypes may specialize on ecological niches outside the ecological optimum of the sexual parents [49].

Some examples of the neotropical flora corroborate the association among apomixis, wide geographic distribution and occupation of habitats with harsh conditions. In Bignoniaceae, some apomictic and polyploid species of *Anemopaegma* [21, 36, 37] and *Handroanthus* [22, 38] show wide geographical distribution and, although they occupy different vegetation types, they are characteristic of *Cerrado*, the neotropical savannas of central Brazil. The majority of apomictic species of *Anemopaegma* compose the *Anemopaegma arvense* complex (*A. acutifolium*, *A. arvense* and *A. glaucum*) that are typical of *Cerrado* areas that suffer constant disturbances, such as fire. As *Anemopaegma* species, *Handroanthus chrysotrichus* and *H. ochraceus* also form an agamic complex typical of the *Cerrado* areas.

Melastomataceae is a predominantly neotropical angiosperm family with many apomictic species [50, 51]. Most of the apomictic species of Melastomataceae belong to the tribe Miconieae and they have wider distributions than the sexual species of the same tribe [51, 52].

5. Genetic variability in apomicts

Traditionally, apomixis is considered a dead end of evolution due to the lack of genetic variability. This view was based on the assumption that loss of heterogeneity in populations would result in loss of potential to adapt to environmental changes [26, 53]. However, recent studies show that is not entirely true. The application of molecular markers in population studies has shown a significant genetic variability in natural apomictic populations, which can often be similar to that of populations of plants with sexual reproduction. Thus, the production of individuals genetically identical to the parental plant (i.e., clones in the strict sense) does not really exist in asexual reproduction [53].

According to Hörandl and Paun [53], different factors such as ancestry of apomictic lineages, backcrossing with sexual relatives, facultative sexuality and mutations contribute to high genetic diversity of apomicts. The ancestry of apomictic lineages defines the initial genetic diversity; thus, allopolyploid origin of most apomicts likely creates initially high levels of heterozygosity. The subsequent evolution of novel genotypes from the original lineages can occur via introgression, facultative sexuality and mutations. Introgression, backcrossing with sexual relatives, can be considered a source for the generation of new genotypes, but it depends on the level of sympatry among the asexual individuals and their sexual relatives. Most apomictic plants show facultative sexuality, which allows the formation of sexual and asexual offspring in the same individual and in the same generation. As a result of these processes of generation of genetic variability, natural apomict populations show greater genotypic variability than expected from a clonal population; however, the frequencies of such sexual events seem to be different among genera, microspecies and even populations of the same species. Finally, the accumulation of somatic mutations might also have a considerable impact on the levels of genetic variation in apomictic groups because of their gradual and continuous accumulation. Although most mutations in coding regions may have deleterious effects, the buffering effects of heterozygosity (allopolyploid origin) and the purging effects of facultative recombination (introgression plus facultative sexuality) have to be taken into account to reduce these effects.

In apomictic plants, genotypic diversity is partitioned more among than within populations [53]. However, studies of genetic diversity in populations of tropical apomictic plants, with polyembryonic seeds and supranumerary embryos formed by adventitious embryony, show a variation in this pattern and it seems to be species-specific. Larger variation was reported among populations of *Eriotheca gracilipes* (Bombacoideae-Malvaceae [41]) and *Garcinia mangostana* (Clusiaceae; [40]). However, in the *Anemopaegma arvense* species complex [54], *Clidemia hirta* [55], *Eriotheca pubescens* [41], *Handroanthus ochraceus* (Bignoniaceae; [38]) and *Opuntia ficus indica* (Cactaceae; [56]) were reported to have larger genetic diversity within populations. Apomictic populations of *Eriotheca* species presented values of genetic variability close (*E. pubescens*) or higher (*E. gracilipes*) than those of the conspecific sexual populations [41]. In *Handroanthus ochraceus*, genetic diversity found within the populations was also similar to that of allogamous populations of the species [38]. According to the authors, the dispersion of seeds by wind of the *Anemopaegma*

species, *Eriotheca* species and *Handroanthus ochraceus* can lead to an increase in intrapopulation diversity, and it can also be responsible for the reduction of interpopulation differentiation due to the greater efficiency of the gene flow [38, 41, 54].

6. Apomixis as promoter of diversity

Apomixis seems to be taxonomically widespread in angiosperms with no clear tendency to specific groups [14, 26]. Despite the three large families Asteraceae, Poaceae and Rosaceae containing the majority of the known apomict-containing genera [26, 57], recent phylogenetic reconstructions of the major clades of angiosperms support the view of a broadly scattered distribution of apomixis over the entire phylogeny [58]. According to the survey carried out by Hojsgaard et al. [26], apomixis was registered in 32 orders (52%), 78 families (19%) and 293 genera (ca. 2.2%).

Some evidences like the presence of apomixis in highly diverse and cosmopolitan clades indicate that the apomixis can be considered a promoter of the diversification and evolution in angiosperms. As mentioned above, apomixis is usually closely related with hybridization and polyploidization events. Plant groups formed by these three processes are called agamic complexes. Such agamic complexes generally present wide distribution, which is related to the greater capacity of apomictic taxa of such complexes that occupy new ecological and geographical niches. It has been hypothesized that high levels of heterozygosity coupled to facultative sexuality and mutations increase genetic diversity and adaptive potential of apomict taxa. In addition, Carman [14] proposed a model for apomixis as facilitator of diversification through cycles of polyploidy and reversions to sex. According to this hypothesis, apomictic polyploids serve as pioneer explorers of new niches whereby they rapidly expand the distribution areas of their progenitor sexual populations by occupying new ecological and geographical niches. Thereafter, reversals to complete sexuality, accompanied by and possibly caused by substantial cytogenetic and genomic perturbations, allow for the establishment of new sexual populations in new habitats without the long-term disadvantages of asexuality [14, 26, 47, 58].

Studies on apomixis in tropical species are scarce and concentrated in few plant families such as Bignoniaceae, Malvaceae, Melastomataceae and Orchidaceae; however, there is a trend of the occurrence of apomict and polyploid taxa in more diverse clades of such neotropical families, as demonstrated by Hojsgaard et al. [26]. In Bignoniaceae, apomict and polyploid taxa were observed in *Anemopaegma* [21, 36] and *Handroanthus* [22, 38]. *Anemopaegma* includes 47 species of shrubs and lianas, representing the third largest genus of the tribe Bignonieae; polyploidy and apomixis were registered in shrub taxa that form the agamic complex called *Anemopaegma arvense* species complex [21, 29, 36, 59] and they show wide geographic distribution in neotropical savanna areas. In the genus *Handroanthus* with 67 species, polyploid and apomictic populations were observed in *H. chrysotrichus* and *H. ochraceus*; the first two species are interfertile and intermediate morphotypes are found in populations of both species. In Malvaceae, polyploidy associated with apomixis has been reported in *Eriotheca* species [20, 38]. Malvaceae is the most diverse family of the Malvales. Melastomataceae is the seventh

largest family of flowering plants, with 170 genera and 5105 species of which some 3000 are neotropical; apomictic species of this family seems to be concentrated in the tribe Miconieae (88%). In Orchidaceae, apomixis is also associated with polyploidy and polyembryony and predominate in tropical species of this family [30].

7. Conclusions

Despite the predominance of sexual reproduction in tropical species, a growing number of studies have shown a reproductive mosaic in such species, with sexual and asexual reproduction in the same species in different populations. In predominant plant families of neotropical vegetation, apomixis, the asexual reproduction via seed, is closely related to polyploid taxa. In addition, adventitious embryony is the prevalent type of apomixis in several plant families that produce polyembryonic seeds and that show wide geographic distribution.

Although several studies have been conducted in recent years, knowledge on the distribution of apomixis in tropical taxa is still scarce and fragmentary. Most of the studies are concentrated in a few families such as Bignoniaceae, Malvaceae, Melastomataceae and Orchidaceae. Even in these more exploited families, only taxa of some clades had their reproductive system elucidated. Thus, I emphasize the need for further studies on the reproductive biology coupled with analyses of ploidy level in tropical species, especially at the population level. Studies concerning the genetic diversity of species that present a mosaic of reproductive systems should also be carried out along the geographical distribution of the species.

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